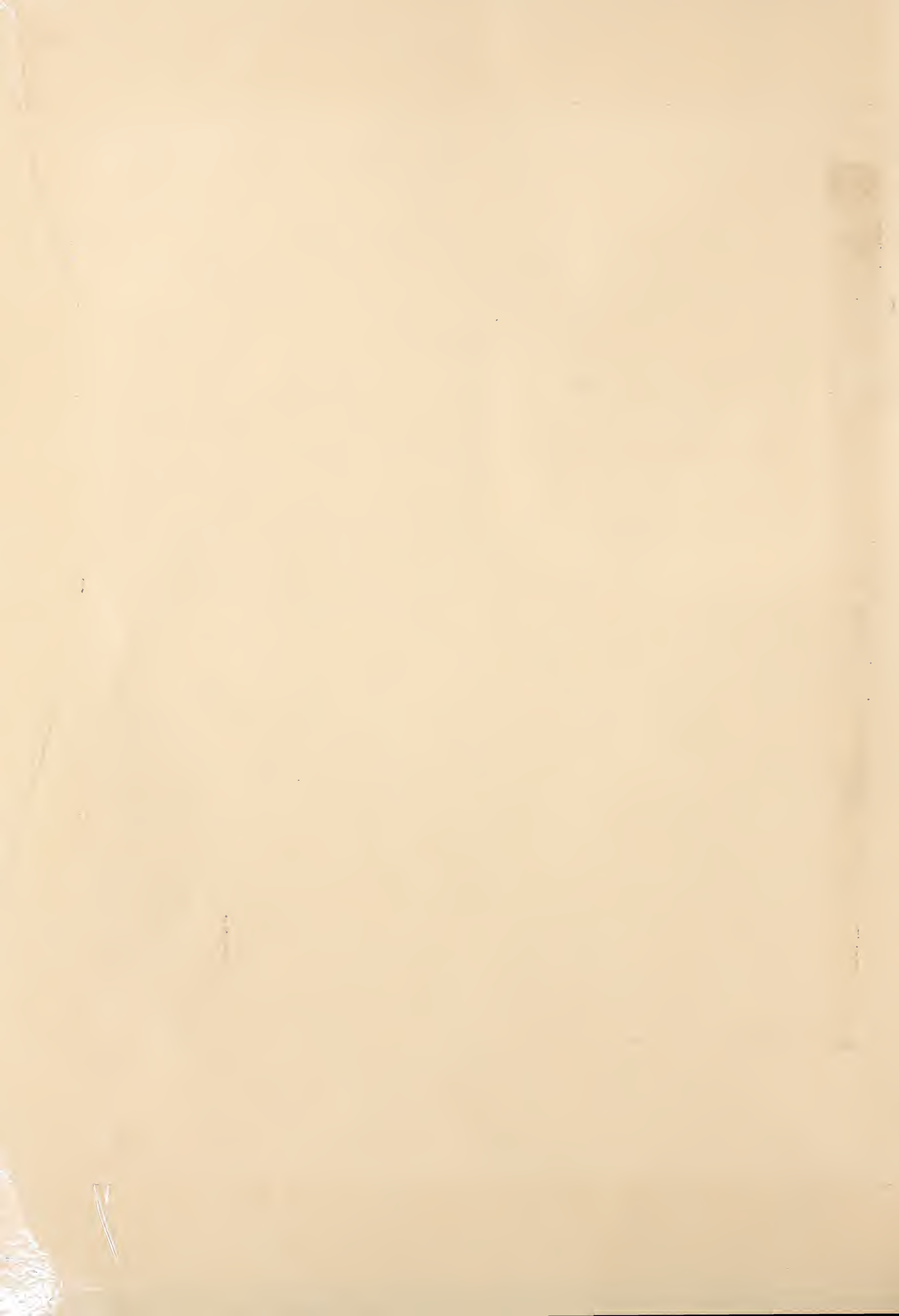


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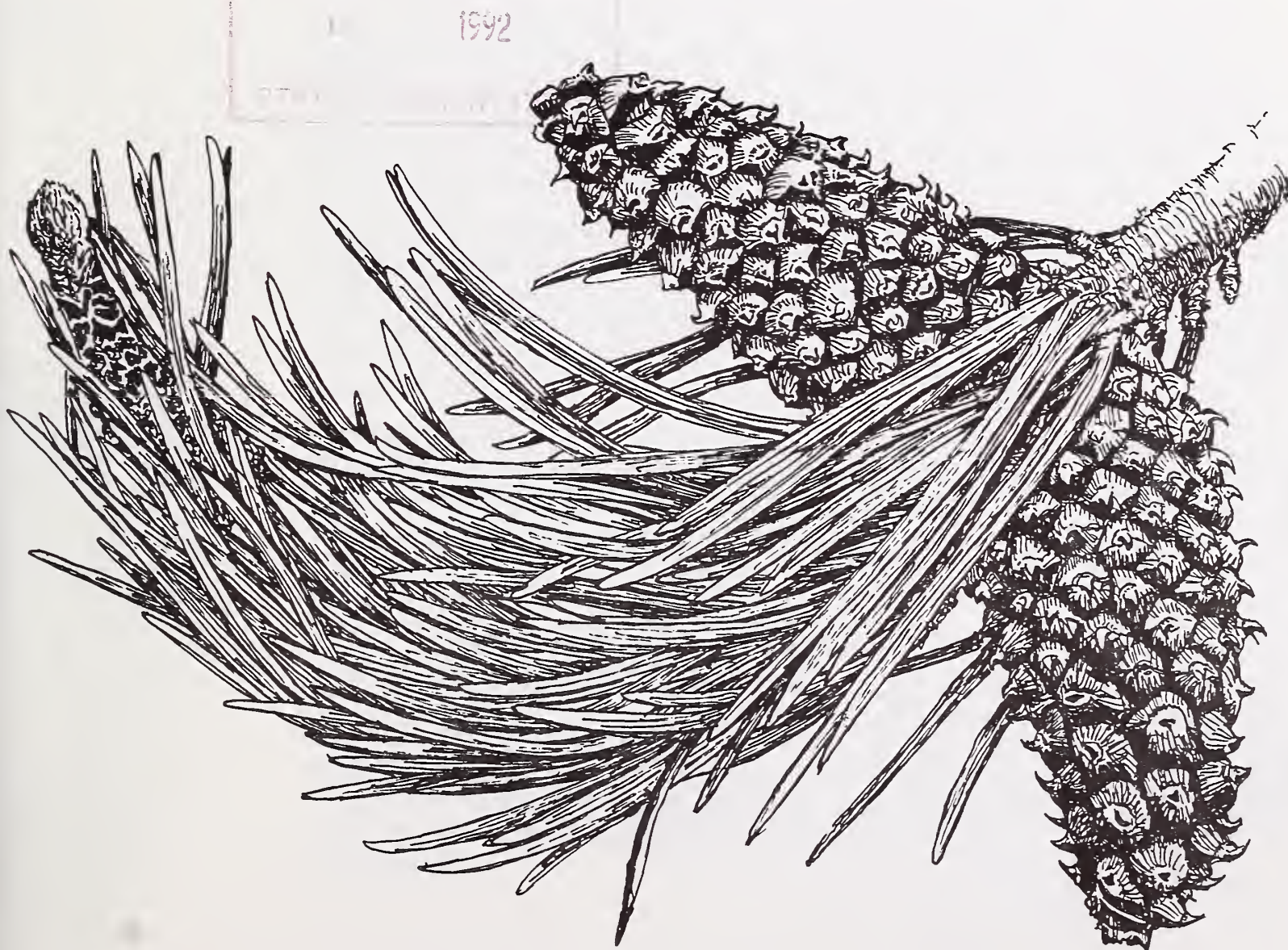
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Genetic Variation and Seed Transfer Guidelines for Lodgepole Pine in Central Oregon

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Abstract

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Cones were collected from 272 trees at 189 locations uniformly distributed over the east slopes of the Oregon Cascade Range and Warner Mountains. Variation in seed and seedling traits was related to (1) seed source latitude, distance from the Cascade crest, elevation, slope, and aspect in multiple regression analyses; and (2) seed zone and elevation band in classification analyses. Provisional seed transfer guidelines are presented. These include a regression equation for guiding seed transfer and estimating transfer risk, and a new outline of fixed seed zones.

Keywords: *Pinus contorta* var. *murrayana*, lodgepole pine, geographic variation, seed transfer, breeding zones.

Summary

Wind-pollinated cones were collected from 272 trees at 189 locations uniformly distributed over the east slopes of the Oregon Cascade Range and southeast into the Warner Mountains. Seed size, germination traits, and seedling growth traits in four environments were related to (1) seed source elevation, latitude, distance from the Cascade crest, slope, and aspect in multiple regression analyses; and (2) seed zone and elevation band in classification analyses.

Two principal components (PCs) were derived from seed and plant traits. The largest component was composed of seedling size and vigor characteristics and differed primarily with elevation of the source. The second component included positive loadings from seed and root size and negative loading from relative shoot elongation during the second year; it differed with latitude and distance from the crest and to a lesser extent with elevation.

Multiple regression equations relating factor scores to geographic variables explained 58 and 36 percent of the source-related variation in PC-1 and PC-2, respectively. In classification analyses using seed zones, 300-m bands in zones and sources in bands, zones, and bands explained about two-thirds of the source-related variance in both principal components. Lack of fit to the geographic models was significant in all analyses.

Provisional seed transfer guidelines are presented. Use of regression equations in guiding seed transfer and estimating transfer risk (percentage of potentially maladapted seedlings) is illustrated. New fixed zones also are proposed in which the original 24 seed zones are placed into seven larger units called regions. Calculations indicated that within these units (300-m elevation bands within either zone or region), the average seed transfer would result in about 20 percent potentially maladapted seedlings. Maximum risk estimates for transfers within a unit were a little in excess of 50 percent.

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Introduction

Lodgepole pine (*Pinus contorta* Dougl. ex Loud.) is a widespread conifer with broad ecological amplitude (Critchfield 1980, Volland 1985). Based on several morphological and isozyme studies, the species has been subdivided into three major groups: coastal (var. *contorta*), Rocky Mountain-Intermountain (var. *latifolia*), and Sierra-Cascade north to the Columbia River (var. *murrayana*) (Critchfield 1980). There is some indication from isozyme analysis that Cascade lodgepole pine south of the Columbia belongs with var. *latifolia* (Wheeler and Guries 1982), but based on seed and cone characteristics and plant vigor, it seems better considered as a component of var. *murrayana* (Critchfield 1957, Stephan 1980, Wheeler and Guries 1982).

Range-wide geographic variation in lodgepole pine has been the subject of many provenance tests (Critchfield 1980), but var. *murrayana* often has been represented by only one or a few sources. Also, plantations in these tests usually have been established north of the natural range of var. *murrayana*. In these trials, *murrayana* sources had heavier seeds (Biot 1978), were slower growing (Dietrichson 1970, Larsen and Nielsen 1982, Lines 1966, Rehfeldt 1985, Stephan 1982), and were less cold hardy (Dietrichson 1970, Rehfeldt 1985) than other inland provenances.

Investigation of geographic variation in lodgepole pine to develop seed transfer guidelines has involved mostly *latifolia* (Rehfeldt 1987, 1988, and elsewhere; Ying and others 1985). These tests show large differences among provenances grown in common gardens. Ying and others (1985), on the basis of field plantations, noted that the species seemed to be plastic and that low- to mid-elevation transfers of 3 degrees in latitude and 400 m in elevation had succeeded through 10 years. In the northern Rocky Mountains of the United States, lodgepole pine has a wide elevational range. Common garden tests (Rehfeldt 1985, 1987, 1988) indicated significant elevational differentiation and that elevational clines could be curvilinear to nearly linear, depending on trait and location within the species range. Geographic clines were gentler: depending on the trait, the amount of differentiation associated with 300 m in elevation ranged from half to twice that associated with 2.1 degrees of latitude (Rehfeldt 1987).

In the Pacific Northwest, lodgepole occupies a variety of habitats near the coast. Inland, it is an important seral species on the drier eastern slopes of the Cascades, but it also may form extensive edaphic or topographic climax forests (Franklin and Dyrness 1973). The present study focuses on genetic variation from the California-Oregon border (42°00' N.) to the Columbia River (ca. 45°40' N.) on the east slopes of the Cascade Range and east to the Warner Mountains in southern Oregon; a few samples from the Ochoco Mountains in central Oregon are included (fig. 1).

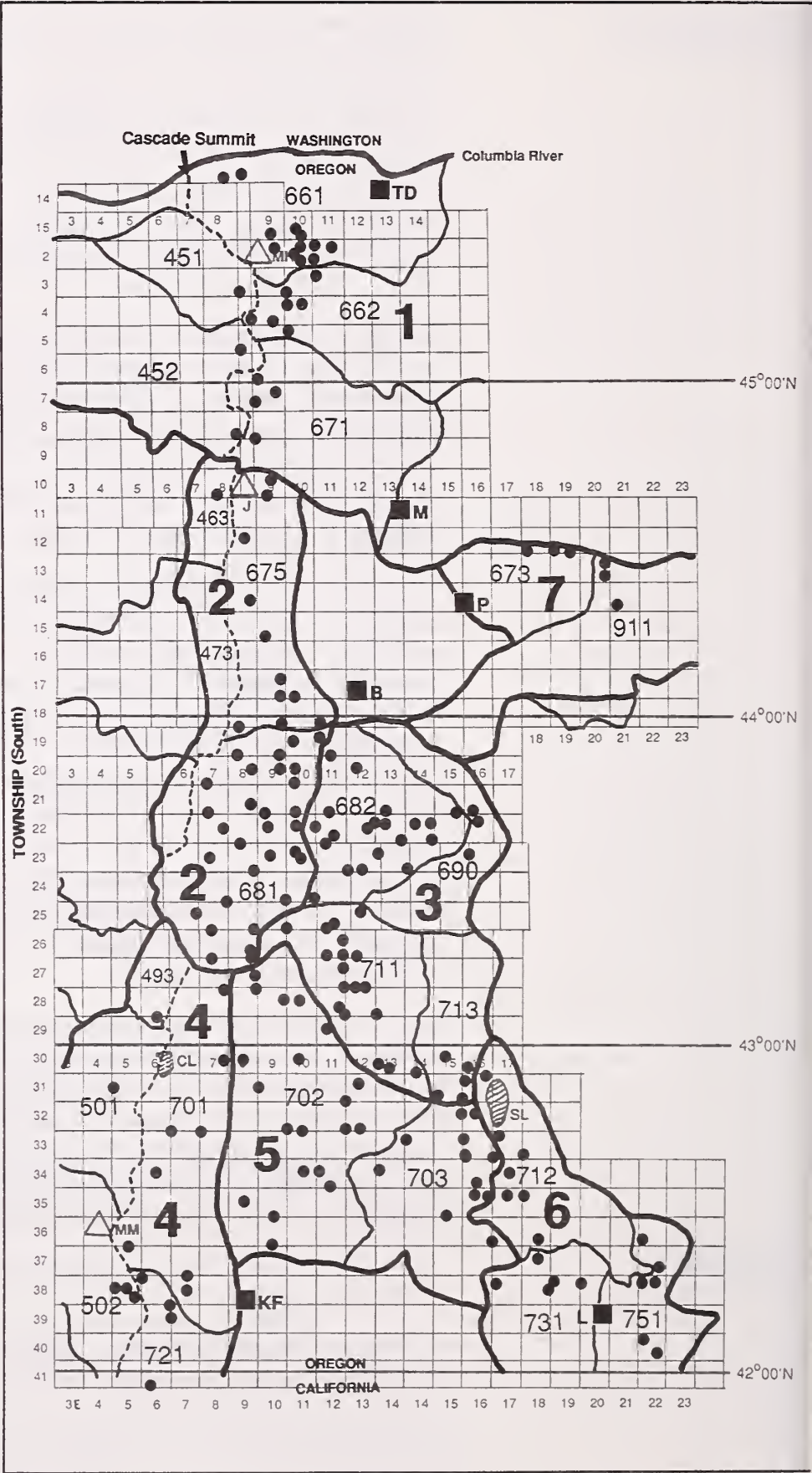
Purposes

The tests investigated source- and family-related genetic variation and had three main purposes:

1. To describe from common garden studies the genetic-geographic pattern of variation in seed germination and in seedling growth and morphology.
2. To relate the pattern of variation to the zones depicted on the current Tree Seed Zone Map (1973).
3. To provide provisional guidelines for seed transfer in artificial regeneration and for breeding zone delineation in the event that current zones are not appropriate.

Stoneman (1984) previously reported on adaptive variation within the southern half of this area with emphasis on zones 701, 702, 703, 711, and 713 (fig. 1).

Figure 1—Map of study area in Oregon Cascade Range and central Oregon. Small squares are townships, about 10 kilometers square. Solid circles are sample locations to nearest quarter of a township. Range numbers (3 E. through 23 E.) are given on the horizontal lines; township numbers (1 N. through 41 S.) are on the left margin. Small outlined areas with three-digit numbers are current seed zones. Larger areas with heavier outlines are proposed zones. Identified towns (solid squares) are TD (The Dalles), M (Madras), P (Prineville), B (Bend), KF (Klamath Falls), and L (Lakeview). Other identified features are the Cascade crest (dashed line), CL (Crater Lake), SL (Summer Lake), and several Cascade peaks (open triangles) from north to south, MH (Mount Hood), J (Mount Jefferson), and MM (Mount McLoughlin).



Materials and Methods Sampling

Collections of wind-pollinated cones were made at 189 locations on the east slopes of the Cascade Range and in the Warner and Ochoco Mountains (fig. 1). At 83 locations, cones were collected from two trees separated by more than 50 m but that represented the same site conditions. These 83 pairs were used to obtain average estimates of variance among families-in-locations and to test for lack of fit to the geographic models. The remaining 106 locations were represented by single families.

To organize cone collection, the area was subdivided by townships (squares of approximately 10 000 ha). Cones were collected in about 80 percent of these townships in which lodgepole pine was present. In addition, collections were made at more than one location in several townships to sample local variation in elevation and site. Some additional collections also were made at the extremes of the range.

The following information was obtained for each sample site: latitude (in degrees), distance from the crest of the Cascade Range (in kilometers), elevation (in meters), aspect (in degrees from north), slope (in a percentage) and "seed zone" (Tree Seed Zone Map 1973).

For some analyses, sample sites also were classified by (1) elevational bands of 200-, 300-, or 400-m widths starting at 765 m; (2) slope categories of flat (0 to 3.5 percent) vs inclined (≥ 3.5 percent); and (3) conifer vegetation groups.

The slope contrast was used because lodgepole pine often occupies flat terrain associated with severe cold air accumulation (Cochran and Berntsen 1973, Cochran and others 1967) or poor moisture drainage (Tarrant 1953). The conifer groups were used because they were easy to classify and, in the field, seemed intuitively related to potentially important site differences. Four groups were recognized:

1. Lodgepole pine plus one or more of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), noble fir (*A. procera* Rehd.), Shasta red fir (*A. magnifica* var. *shastensis* Lemm.), whitebark pine (*Pinus albicaulis* Engelm.), western white pine (*P. monticola* Dougl. ex D. Don), and mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.). This group might have a small component (<5 percent based on mature trees) of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) or sugar pine (*Pinus lambertiana* Dougl.). It was generally an upper-slope grouping.
2. Lodgepole pine only.
3. Lodgepole pine plus ponderosa pine only.
4. Lodgepole pine plus one or more of white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.), incense-cedar (*Calocedrus decurrens* (Torr.) Florin), western juniper (*Juniperus occidentalis* Hook.), western larch (*Larix occidentalis* Nutt.), sugar pine, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western redcedar (*Thuja plicata* Donn ex D. Don), and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). This group might include ponderosa pine and a small component (<5 percent) of the species listed in group 1.

Group (1) was, on average, more northerly, closer to the Cascade crest, and about 300 m higher in elevation than the other three, whose distributions for the most part overlapped. The lodgepole pine group (2) often occurred on the flats (32 of 43 locations).

Table 1—Frost-free season (days between frosts of -2.2 °C), mean annual precipitation, and deficits in water balance (maximum deficit and number of months during which deficit was measured) at several weather stations in and east of the Cascade Range

Weather station	Latitude	Longitude	Distance ^a	Elevation	Frost-free season	Precipitation	Water deficit	
							Maximum	Months
	°N	°W	Km	Meters	Days	— — Millimeters ^b — —		No.
Government Camp	45°20'	121°47'	-7	1140	—	2160	100	2
Lapine	43°40'	121°29'	37	1335	—	360	360	7
Odell Lake	43°35'	122°03'	2	1460	121	1530	200	4
Crescent	43°27'	121°42'	32	1360	—	490	310	7
Chemult	43°14'	121°47'	20	1450	11	680	280	6
Round Grove	42°20'	120°53'	110	1490	74	410	310	7

— = no record.

^a Distance east of Cascade crest; negative is west.

^b Inches = millimeters ÷ 25.4.

Climatic Variation

Weather stations are uncommon near lodgepole pine sites, but table 1 lists records from several stations that show the range of conditions between the High Cascades and the approaches to the High Desert (Johnsgard 1963). This small sample indicates that the environmental variability is great; even among weather stations at comparable elevations, differences in precipitation and growing season are remarkable. Precipitation decreases rapidly from west to east and more gradually from north to south. South of about 43° N. latitude, the Siskiyou Mountains extend west to the coast; they probably extract more moisture from incoming storms before those storms reach the Cascades than occurs farther north (Froehlich and others 1982, Miller 1972).

Seed Traits

Seed weight—Seed weight was based on two 25-seed samples of filled seeds, as determined from x ray images.

Mean and standard deviation of germination rate—Two 50-seed samples from each family were soaked for 24 hours in aerated distilled water at room temperature (ca. 22 °C), stratified at 2-4 °C for 30 days, and germinated on moist filter paper in covered petri dishes 9 cm in diameter. Incubation was at a constant 15 °C with 12-hour photoperiod. Two replications were placed in separate commercial incubators. Mean rates and standard deviations of rates for seeds within a petri dish were determined by procedures described in Campbell and Sorensen (1979).

Seedling Traits

Seedling traits were measured or observed in four "environments" consisting of 2 years of sowing (1982 and 1983) and two air temperature treatments. One treatment included a plastic tent over the bed from November through April plus supplemental water and fertilizer during the second extension season. The second treatment was not covered and had minimal water and no fertilizer the second year. There were two replications in each environment.

Prior to sowing, seeds were pretreated as for the germination test except that the stratification period was 60 days. Stratified seeds were sown at 8-cm spacing in four-tree family row plots. The test was surrounded by two border rows.

Germination and seedling traits are listed in table 2. For the seedling traits, each of the four environments was analyzed separately (table 3). Because of heterogeneity of within-plot variance for top and root dry weights, these measures were transformed to logarithms before analysis. All means for the seedling traits, except traits 4 and 5 (table 2), were based on four plants per plot.

Components of variance were estimated from each analysis for source (σ^2_s), family-in-source ($\sigma^2_{F/S}$), and error (σ^2) (table 3). In the following presentation $\sigma^2_{F/S} + \sigma^2_s$ is referred to as total family variance and $\sigma^2 + \sigma^2_{F/S} + \sigma^2_s$ as total variance and symbolized, σ^2_T . Family variance as proportion of total variance [$(\sigma^2_{F/S} + \sigma^2_s)/\sigma^2_T$] and source to family-in-source ratio ($\sigma^2_s/\sigma^2_{F/S}$) were calculated for each trait.

Factor-Score Calculation

Because procedures used in this study followed those described by Campbell (Campbell 1986, Campbell and others 1989), only the main points will be noted here. A total of 58 traits were analyzed. Traits with $\sigma^2_s/\sigma^2_T < 0.35$ or that were highly correlated with other traits were deleted. This reduced the number of traits to 24 (table 2). Components of variance and covariance were calculated for each trait and trait pair, respectively (Griffing 1956, Kempthorne 1957), and genetic correlation coefficients were calculated at the source and family-in-source levels (Campbell and others 1989, Morrison 1967). Principal component analysis was run with the matrix of source-level correlation coefficients as input (SAS Institute 1987). Factor scores (FS) were calculated for each family ($n = 272$) from the eigenvectors of the first two principal components. Geographic patterns of genetic variation among parent trees were evaluated by regressing factor scores against site variables or by hierarchal analysis using site classification models.

Regression Analyses

Geographic predictor variables were derived from source elevation, latitude, distance from the Cascade crest, and three slope-aspect transformations. Elevation and latitude were rescaled: elevation = (meters - 800) $\times 10^{-1}$, and latitude = degrees N. - 40. Distance from the Cascade crest in kilometers was used rather than longitude, because the Cascade Range was considered an important climatic determinant for eastern Oregon, and its orientation is not true north-south. Slope was transformed to its tangent and aspect to its east-west [$\tan(\text{slope}) \times \sin(\text{aspect})$] and north-south [$\tan(\text{slope}) \times \cos(\text{aspect})$] deviations (Stage 1976).

Factor scores for families were fitted to a model including 40 linear, quadratic, linear \times linear, and linear \times quadratic terms of the six location variables. Mallows' Cp statistic (Daniel and Wood 1971) was used to select the best unbiased reduced equation (SAS Institute 1987). The residual mean square from the regression of all available predictor variables usually is the best estimate of the residual variance (Snedecor and Cochran 1980). The value of the Mallows' criterion closest to the number of predictors was used to select the final prediction equation.

Table 2—Description of traits and their measurement units

Trait	Description	Units	Selected ^a
Seed traits:			
1. Weight	Based on 2 25-seed samples of filled seeds	Milligrams per filled seed	Yes
2. Germination rate	Calculated from probits	Days ⁻¹ to 50% germination	Yes
3. Standard deviation of 2	Calculated from probits	Stand. dev. of days ⁻¹	Yes
Measured seedling traits:			
4. Time to emergence	Based on 20 seeds per plot	Days to 50% emergence	Yes
5. Cotyledon number	Based on 10 seedlings per plot	Cotyledons per seedling	
6. Winter color of primary needles	Scaled from 0 (green) to 4 (dark purple)	Score	
7. Needle length	Total length of mature 2d year fascicle of needles	Millimeters	11,12,21,22
8. Height—1F	Total height at end of 1st year	Centimeters	11,12,21,22
9. Height—2E	Total height at midseason of 2d year	Centimeters	
10. Height—2F	Total height at end of 2d year	Centimeters	
11. Height—2 other	3 additional 2d-year midseason heights (1983 sowing only)	Centimeters	
12. Diameter	Final 2d-year diameter below cotyledons	Millimeters	12,22
13. Top dry weight	Total at end of 2d year	Log _e gram	11,12,22
14. Root dry weight	Total at end of 2d year	Log _e gram	12,22
Derived seedling traits:			
15. Top-to-root ratio	Trait 13 divided by trait 14	Log _e gram/log _e gram	11,12,22
16. Relative elongation rate—2	Log _e trait 10 minus log _e trait 8	Log _e centimeters- Log _e centimeters	
17. Height-to-diameter ratio	Trait 10 divided by trait 12	Centimeters/millimeters	21
18. Early height growth—2	(Trait 9 - trait 8) divided by (trait 10-8)	(Centimeters-centimeters)/ (centimeters-centimeters)	22

^a Traits selected for inclusion in the principal component analyses. "Yes" identifies traits tested in only one environment or not affected by test environment (cotyledon number). For growth traits, the 1st number of the pair indicates year of sowing (1 = 1982, 2 = 1983), the 2d number indicates air-temperature treatment (1 = natural, 2 = beds covered with plastic tent in winter).

A good geographic model for guiding seed transfer should account for most of the source-related variation and there should be no lack of fit to the model (Campbell 1991). Lack of fit to the regression equation is caused by location variation that is not explained by the selected regression model. In the present test, mean square for lack of fit was tested against pooled variance between families in location for the 83 locations represented by pairs of families. Factor scores of the two families at a location served as "repeat" observations for that location (Draper and Smith 1966). Significant lack of fit to the equation indicated variation among sources over and above that explained by the model. This could be due to site factors, such as soils, slope position, and so forth, that are not in the model (Campbell 1991). Presumably it represents, to some extent, adaptive location effects. The goal of the analysis is, without developing a model that overfits, to minimize or eliminate lack of fit in the sense that the unexplained source variance does not exceed the variance among families within a location.

Table 3—Analysis of variance format for individual traits in each environment

Sources of variation	Degrees of freedom	Expected mean squares
Total	543 ^a	
Replications	1	
Sources	188	$\sigma^2 + 2 \sigma^2_{F/S} + 2.8765 \sigma^2_S$
Families-in-sources	83	$\sigma^2 + 2 \sigma^2_{F/S}$
Remainder	271	σ^2

^a In 1-year-environment combination, the total and remainder degrees of freedom were each reduced by 1 because of a missing plot. Coefficients for $\sigma^2_{F/S}$ and σ^2_S were 1.9920 and 2.8712, respectively.

Classification Analyses

Locations were initially classified by seed zone (Tree Seed Zone Map 1973) and 300-m elevation bands within zones. Variance components were estimated from a nested random model:

$$Y_{ijkl} = u + Z_i + E_{ij} + S_{ijk} + F_{ijkl}, \quad (1)$$

where

u = test mean;

Z_i = i^{th} seed zone (fig. 1, units designated with three-digit numbers);

E_{ij} = j^{th} 300-m elevation band within zone;

S_{ijk} = k^{th} seed source within elevation band within zone;

F_{ijkl} = l^{th} family within seed source; and

Y_{ijkl} = the value of the l^{th} family of the k^{th} source in the j^{th} elevation band of the i^{th} seed zone. All subsample levels had unequal numbers with,

$l = 1$ or 2 (mean 1.44) families per source,

$k = 1$ to 14 (mean 3.19) sources per 300-meter elevation band in seed zone,

$j = 1$ to 5 (mean 2.46) elevation bands per seed zone, and

$i = 1, 2, \dots, 24$ seed zones.

Components of variance, σ^2_Z (seed zones), $\sigma^2_{E/Z}$ (elevation bands in zones), and $\sigma^2_{S/E/Z}$ (sources in bands in zones), were estimated for both factor scores. This model assumed that seed zone and elevation band within seed zone explained the variation among locations. Lack of fit to the classification model, therefore, was represented by $\sigma^2_{S/E/Z}$, which was the pooled estimate of variance among locations within elevation bands within zones. As with the regression model, lack of fit was tested against variance among families in locations. If lack of fit is significant, the model can be altered by reclassifying the topography. Several classifications were tried for lodgepole pine.

The preceding model was used with 200- and 400-m bands and values for $\sigma^2_{S/E/Z}$ compared for the three band widths. Next, two other classifications were added separately to the nesting. Only the 300-m band width was used in these analyses. First, flat vs inclined sites within elevation bands within seed zones were contrasted by using the model,

$$Y_{ijklm} = u + Z_i + E_{ij} + T_{ijk} + S_{ijkl} + F_{ijklm}, \quad (2)$$

where

$T_{ijk} = k^{\text{th}}$ slope type (flat or inclined) within elevation band within zone, and

Y_{ijklm} = the value of the m^{th} family of the i^{th} source in the k^{th} slope type in the j^{th} elevation band of the i^{th} zone.

Second, the four conifer groups were included,

$$Y_{ijklm} = u + Z_i + E_{ij} + C_{ijk} + S_{ijkl} + F_{ijklm}, \quad (3)$$

where symbols are as in equation (2), except that C_{ijk} symbolizes the k^{th} conifer association. The analysis nested the four associations within elevation bands within seed zones.

Finally, regression analyses indicated that, in some parts of the study area, current seed zones may be overly conservative in regulating seed transfer. Several attempts were made to group zones based on visual inspection of plots of the regression equations (see below) and three-dimensional contour plots (Becker and others 1988) of the factor scores. Where mapped contours indicated flat or gentle latitudinal and distance gradients, seed zones (Tree Seed Zone Map 1973) were combined into larger groups designated "regions" and analyzed by using the model,

$$Y_{ijkl} = u + R_i + E_{ij} + S_{ijk} + F_{ijkl}, \quad (4)$$

where

$R_i = i^{\text{th}}$ seed region (fig. 1, units with bold outlines and numbered 1 - 7); and

Y_{ijkl} = the value of the l^{th} family of the k^{th} source in the j^{th} elevation band in the i^{th} region.

Components of variance from this model were σ^2_R (seed regions), $\sigma^2_{E/R}$ (elevation bands in regions) and $\sigma^2_{S/E/R}$ (sources in bands in regions).

Comparisons of Regression and Classification Analyses

Subzones (300-m elevation bands within seed zones) and subregions (300-m elevation bands within seven regional groupings of seed zones [fig. 1]) were included separately as "dummy" variables (Draper and Smith 1966) in the geographic regression model (Campbell 1991). Both classification and geographic regression analyses, as will be shown later, had significant lack of fit. The combined analyses, therefore, had two purposes: (1) to significantly reduce or eliminate lack of fit, and (2) to determine if topographic variables still removed significant source-related sums of squares after the contribution of subzones had been removed.

Estimation of Transfer Risk

In calculating seed-transfer risk (R), I attempted to estimate the adaptive genetic “mismatch” between the population of seedlings being transferred and a population native to the planting site (Campbell 1986). The local population probably always includes extreme types that stabilizing selection removes. Year-to-year climatic fluctuations, among other factors, also may cause different selection over time at the same location. Nevertheless for purposes of estimation, it was assumed that the local population represented adaptation to the site, and deviations from the local population represented to some extent (see below) adaptive mismatch.

Additive genetic variance among pooled families-in-sources was used to scale R . Additive genetic variance was calculated as $3\sigma^2_{F/S}$. The coefficient 3 was used because of the likelihood of pollination among trees within family clusters (Squillace 1974) and because of the observed low level of seed produced by self-pollination in central Oregon lodgepole pine (Sorensen 1987). The value $\sigma^2_{F/S}$ was estimated from locations represented by two families each. It was assumed that the pooled value of these pairs could be applied over the sample area.

In the following presentation, R is the estimated proportion of plants in the seedling population that is, in the course of a rotation, presumed to be at risk from some type of environmental damage; for example, $R = 0.4$ implies that 40 percent of the seedling population is outside the genetic distribution of the local population and potentially at risk during the life of the stand.

For the classification analysis, average seed transfer risk among locations within elevation bands and zones (R_w) was estimated by assuming that $\sigma^2_{S/E/Z}$ was distributed normally. In this case, mean distance between points under the normal curve was calculated as (Patel and Read 1982),

$$X_d = \sigma_{x_i-x_j} (2/\pi)^{1/2},$$

which simplifies to

$$X_d = 2\sigma_{S/E/Z} (1/\pi)^{1/2},$$

where

X_d = mean distance between two random points within a normal distribution,

x_i and x_j = random points, and

$\sigma_{S/E/Z}$ = standard deviation of the appropriate component of variance from the classification analysis.

The estimate of $\sigma^2_{S/E/Z}$ included, in addition to adaptive variation within elevation band and zone, sampling error associated with sample sizes of one and two families per location plus genetic effects such as drift and nonlocal wind pollination. Judging the contribution of human and genetic sampling errors to $\sigma^2_{S/E/Z}$ was somewhat arbitrary, but I assumed that half of R_w represented sampling errors and half represented adaptive differences associated with transfers among random locations with an E/Z. This was evaluated later by calculating R -values for random transfers among actual sample points within an elevation band and zone.

Risk values have not been field tested. The values are indicators of relative, not absolute, risk. Nevertheless, for the purpose of field guidance I have used as "safe" an $R \leq 0.51$, which is based on $R = 0.3$ for the two principal components (PCs) individually. This implies that ≤ 51 percent of the planted seedlings are mismatched to the planting site and potentially at risk. As an illustration, I will use the assumptions that field planting is at 3.05-m spacing (1080 trees per ha), that 30 percent (325 plants per ha) are lost due to early mechanical damage (trampling, browsing, soil slippage, windfalls, and so forth), that desired crop density at harvest is 300 trees per ha, and that there should be a little cushion for the unexpected. These assumptions result in a harvest of 40 percent of the seedlings that escape mechanical damage $\{300 \text{ crop trees} / [1080 \text{ planted seedlings} - (0.3)(1080)] = 0.40\}$, or 60 percent of plants could be environmentally impacted and the harvest target of 300 adapted trees per ha still met. Site class, rotation age, commercial thinning, and different estimate of mechanical damage could alter the acceptable risk.

Results

Geographic Distribution of Lodgepole Pine Sites

With the exception of a few locations west of the crest and a few in the Ochoco Mountains (fig. 1, seed zones 673 and 911), the sample area was bordered on the west by the Cascade summit and on the east by the approaches to the High Desert (fig. 1). Mean sample elevation was 1600 m; minimum 820 m, maximum 2450 m. Local elevational ranges were sometimes great with the maximum range within a single seed zone of 1120 m. Twenty-eight percent of the locations were on flat ground. Of the remainder, 26, 31, 23, and 20 percent were northeast, southeast, southwest, and northwest exposures, respectively, not significantly different from an equal distribution (chi-square = 3.86, d.f. = 3, $p > 0.25$). Mean slope was 7 percent with the distribution strongly skewed to shallow slopes. Seventy-eight percent of the sample locations had slopes < 11 percent, and only 6 percent of the locations had slopes > 20 percent. Steepest slope was 45 percent.

Many of the following geographic variables identifying locations of the sample sites were intercorrelated, but associations between them (R^2) generally were small (table 4):

1. Distance decreased with latitude, because the range of lodgepole was narrower at higher latitudes (fig. 1).
2. Elevation decreased with latitude and increased with distance from the Cascades. Although there was a decrease in elevation immediately east of the Cascade crest, the land mass in general increased in elevation toward the south and east.
3. Sample locations tended to more westerly aspects in the south and farther from the Cascades.
4. Steeper slopes tended to be at higher elevations, and there was a slight tendency for sample locations to be on northerly aspects on steeper slopes and on southerly aspects on shallower slopes.

Table 4—Linear correlation coefficients between latitude (L) in degrees, distance (D) from the Cascade crest in kilometers, elevation (E) in meters, aspect variables (A) and (B) and slope (T) in percent

Geographic variables	Geographic variables				
	D	E	A ^a	B ^b	T
L	-0.481***	-0.493***	0.241***	-0.082	0.093
D		.546***	-.118*	.039	-.099
E			-.091	-.036	.231***
A				-.013	.058
B					.148*

* = $p < 0.05$; *** = $p < 0.001$.

^a East-west deviation of aspect, $\tan(\text{slope}) \times \sin(\text{aspect})$.

^b North-south deviation of aspect, $\tan(\text{slope}) \times \cos(\text{aspect})$.

Year and Treatment Effects

Final seedling sizes differed between years of sowing and between treatments. Seedlings from seeds sown in 1983 were 14 percent taller and 16 percent larger in caliper than seedlings from seeds sown in 1982.

Seedlings under the plastic tent from midautumn to midspring were 24 percent taller, were 21 percent larger in caliper, and had 40-percent-heavier tops (back transformed from natural logs) than uncovered seedlings. Also in the covered seedlings, relative elongation the second year was greater by 35 percent and needles were longer by 8 percent. Plants covered in winter were, on average, a little stockier (smaller height-diameter ratio) than plants not covered, but the two groups did not differ in top-root ratio when root and shoot weights were expressed in logarithms of dry weights. Periodic measurements of a small sample of seedlings indicated that terminal buds of seedlings under the tents commenced elongation 2 to 3 weeks earlier than buds of seedlings in the open.

Relations Among Traits

Genetic correlations among traits differed greatly but generally were larger by a factor of 2 when based on source components than when based on family-in-source components.

For two pairs of traits, correlations based on sources contrasted strongly with those based on families-in-sources. The four coefficients between mean emergence time (not in principal component analysis) and final height were -0.477, -0.495, -0.563, and -0.513 (mean, -0.512) based on source, but +0.443, +0.322, +0.423, and +0.521 (mean, +0.427) when based on families-in-sources. At the source level, rapid emergence was associated with relatively short 2-year seedlings; at the within-source level, it was associated with relatively tall 2-year seedlings. In a similar contrast, relative height elongation in year 2 had, on average, a high positive correlation with final height at the source level (mean of four environments, +0.812) but no correlation at the family-in-source level (mean, -0.036).

Factor Scores

Because the purpose of the study was to describe adaptive variation, the principal component analysis was based on the source correlation matrix. The analysis reduced the complex and highly correlated system of 24 seed and seedling traits (table 2, last column) by creating two principal components that explained 90 percent of the source variation in the 24 traits. PC-1 (eigenvalue 19.11) explained much more of the variation than PC-2 (eigenvalue 2.40) (table 5). Trait communalities showed how much of the variation in the trait was accounted for by the two principal components. The large values (table 5) indicated that the two PCs accounted for most variation in all traits except germination rate. Recent tests with Douglas-fir (Sorensen, manuscript in preparation) and ponderosa pine seed (Ager and Stettler 1987, Weber 1988) suggest that germination rate may include more local microsite adaptive variation than do seedling traits.

The two factor scores for a family (one for each principal component) represented the mean genotypic value for the family based on the 24 traits. The first principal component reflected primarily vigor as shown by the loadings for needle and size traits (table 5), but early growth and height-diameter ratio also loaded heavily for this factor score. The signs indicate the "direction" of loading. Thus a large factor score for PC-1 meant a family had large seedlings with long needles, was relatively stocky (low height-diameter ratio), and started elongation relatively late in spring (little elongation had occurred at the time of the first height measurement in the second year). The second principal component loaded heavily for seed weight and cotyledon number, moderately and negative for relative elongation rate, and in the covered beds, heavier for root than for top dry weight (table 5). A large factor score for PC-2 indicated a family with heavy seeds, many cotyledons, little second-year elongation for first-year height, and large root dry weight relative to top dry weight.

Regression Analyses

Simple regression coefficients relating principal components to geographic variables (table 6) showed that factor score-1 (FS-1) was more strongly related to elevation and FS-2 more strongly related to latitude and distance.

Multiple regression equations relating factor scores to geographic variables were very complex. Major location variables (latitude, distance, and elevation) were by far the most important (table 7). Slope also entered into the equation for PC-1, but standard coefficients for the terms involving slope were small. Results for the two PCs are given separately.

PC-1—The equation explained 58 percent of the source-related variation. Many of the significant geographic terms involved interactions or curvilinear responses (table 7). Elevational clines were nearly linear on the east slopes of the Cascades and were most shallow in the south (fig. 2). A risk scale equivalent to one standard deviation of the within-source genetic variation is indicated in figure 2. Transfers of 500 m would not exceed this scale interval near the Cascade summit. Farther east, elevational gradients were steeper and curvilinear, and rate of change in PC-1 increased with elevation (fig. 3). At high elevation in a few parts of the range, transfers of less than 300 m exceeded one standard deviation on the risk scale (for example, fig. 3, 2000 to 2200 m, 43.70° N.), but this was exceptional.

The only appreciable change in PC-1 with latitude occurred near the Cascades at higher elevation (fig. 2). Farther from the crest, the north-south species distribution was more limited, particularly if the Ochoco Mountains were excluded, and the latitudinal cline was shallow within this distribution (fig. 3).

Table 5—Principal components with trait loadings, coefficients, communalities, eigenvalues and percentages of variation explained

Trait	PC-1 ^a		PC-2 ^b		Communality
	Loading	Coefficient	Loading	Coefficient	
SW ^c	−0.158	0.098	0.941	−0.379	0.910
MGR	−.541	−.031	−.036	.007	.293
SDGR	−.722	−.030	.061	−.035	.526
CN	−.343	.079	.853	−.347	.845
11N	.976	.046	−.028	.025	.954
12N	.974	.046	−.025	.024	.950
21N	1.014	.042	−.081	.047	1.034
22N	.974	.045	−.037	.028	.949
11H	.944	.059	.101	−.027	.902
12H	.946	.066	.163	−.052	.922
21H	1.019	.063	.107	−.029	1.051
22H	.994	.062	.109	−.030	.999
12D	.984	.072	.196	−.065	1.006
22D	1.008	.073	.197	−.165	1.054
11T	.868	.069	.225	−.078	.805
12T	1.004	.063	.113	−.031	1.021
22T	1.002	.064	.120	−.034	1.018
12R	.927	.080	.293	−.104	.945
22R	.988	.075	.229	−.077	1.029
21HD	−.989	−.026	.215	−.100	1.025
22EG	−.802	−.036	.041	−.028	.646
11RER	.797	−.006	−.410	.176	.804
12RER	.889	.012	−.293	.130	.876
22RER	.911	.007	−.345	.151	.949

^a Eigenvalue = 19.111; percent of variation = 79.6.

^b Eigenvalue = 2.410; percent of variation = 10.0.

^c Symbols representing the traits are identified in table 2.

Table 6—Partial simple regression coefficients between the factor scores for the 2 principal components and 5 geographic or topographic variables

Geographic or topographic variable	FS-1	FS-2
Latitude	0.026	0.487***
Distance from Cascade crest	−.138*	−.410***
Elevation	−.599***	−.330***
Aspect:		
East-west deviation	.058	.147*
North-south deviation	.081	−.013
Slope	.198**	.131*

* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

Table 7—Regression equations relating factor scores of principal components to geographic variables

Principal component 1 ^a				Principal component 2 ^c			
Variable ^b	Partial coefficient	Significance p<	Standard coefficient	Variable ^b	Partial coefficient	Significance p<	Standard coefficient
E	3.68-02	0.001	1.38	D	-9.46-03	0.001	-0.45
S	-2.02-02	.001	-.22	E	-1.32-01	.001	-4.13
D ²	-2.40-04	.001	-1.98	L	-5.37	.001	-5.16
DL	1.63-02	.001	2.72	E ²	-1.06-04	.081	-.58
EL	-2.45-02	.001	-2.92	L ²	7.84-01	.001	5.81
DE ²	-1.65-06	.001	-1.45	EL	8.69-02	.001	8.67
D ² E	1.69-06	.003	1.66	D ²	4.96-07	.014	.41
DL ²	-2.24-03	.001	-1.35	EL ²	-1.20-02	.001	-5.93
EL ²	2.81-03	.001	1.66	Const	8.24	.001	
LS ²	2.12-04	.003	.29				
Const	7.15-01	.001					

^a Probability of lack of fit of PC-1 is 0.002 (d.f. = 178,83; F = 1.75). R² = 0.584.

^b D = distance from Cascade crest in kilometers. E = elevation in (meters - 800)/10. L = latitude in °N - 40. S = slope in tan (slope) = percent/100.

^c Probability of lack of fit of PC-2 is 0.040 (d.f. = 180,83; F = 1.41). R² = 0.364.

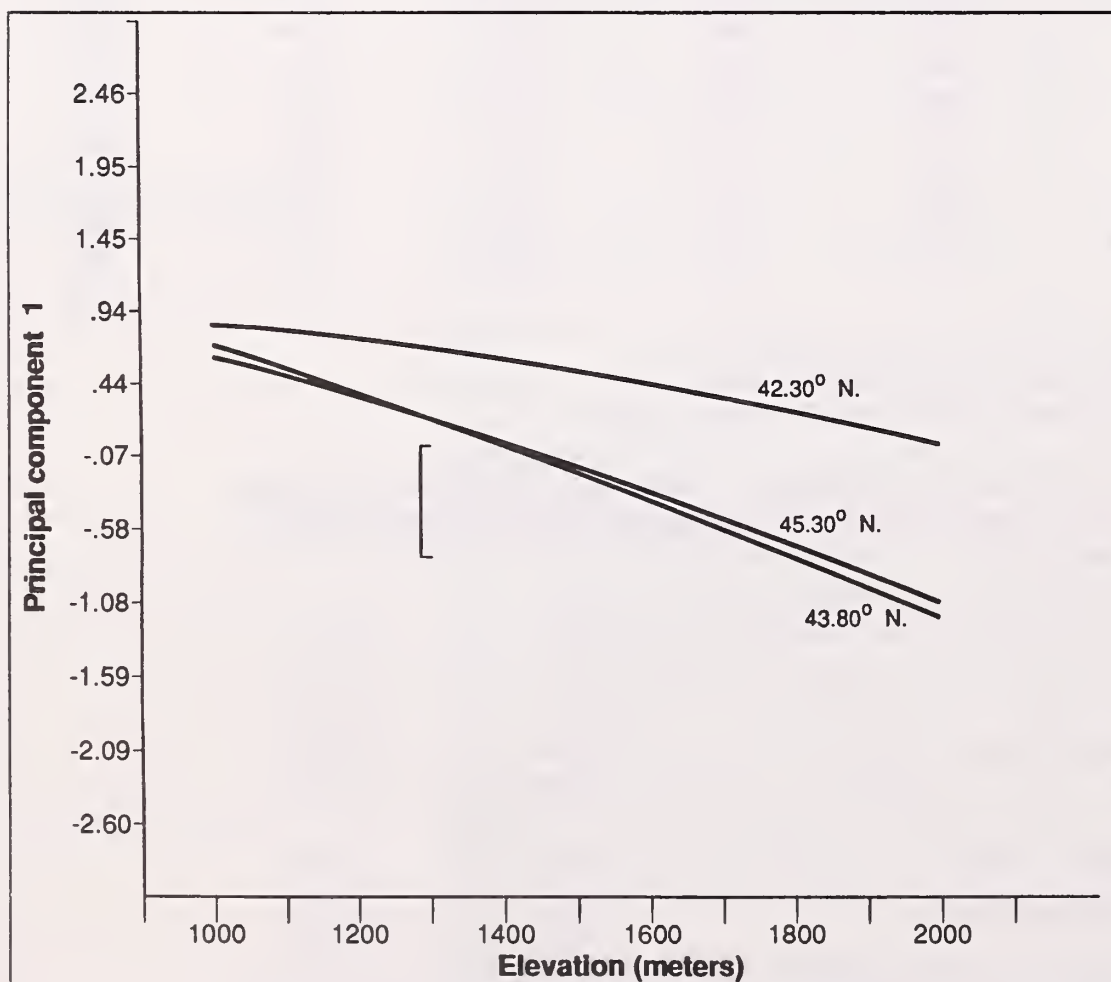


Figure 2—Relation between principal component 1 and elevation at three latitudes, other factors constant at slope = 7 percent and distance = 15 kilometers east of Cascade crest. Vertical line is equal to one standard deviation of within-source additive genetic variance of principal component -1 and is equivalent to a transfer risk of 0.38.

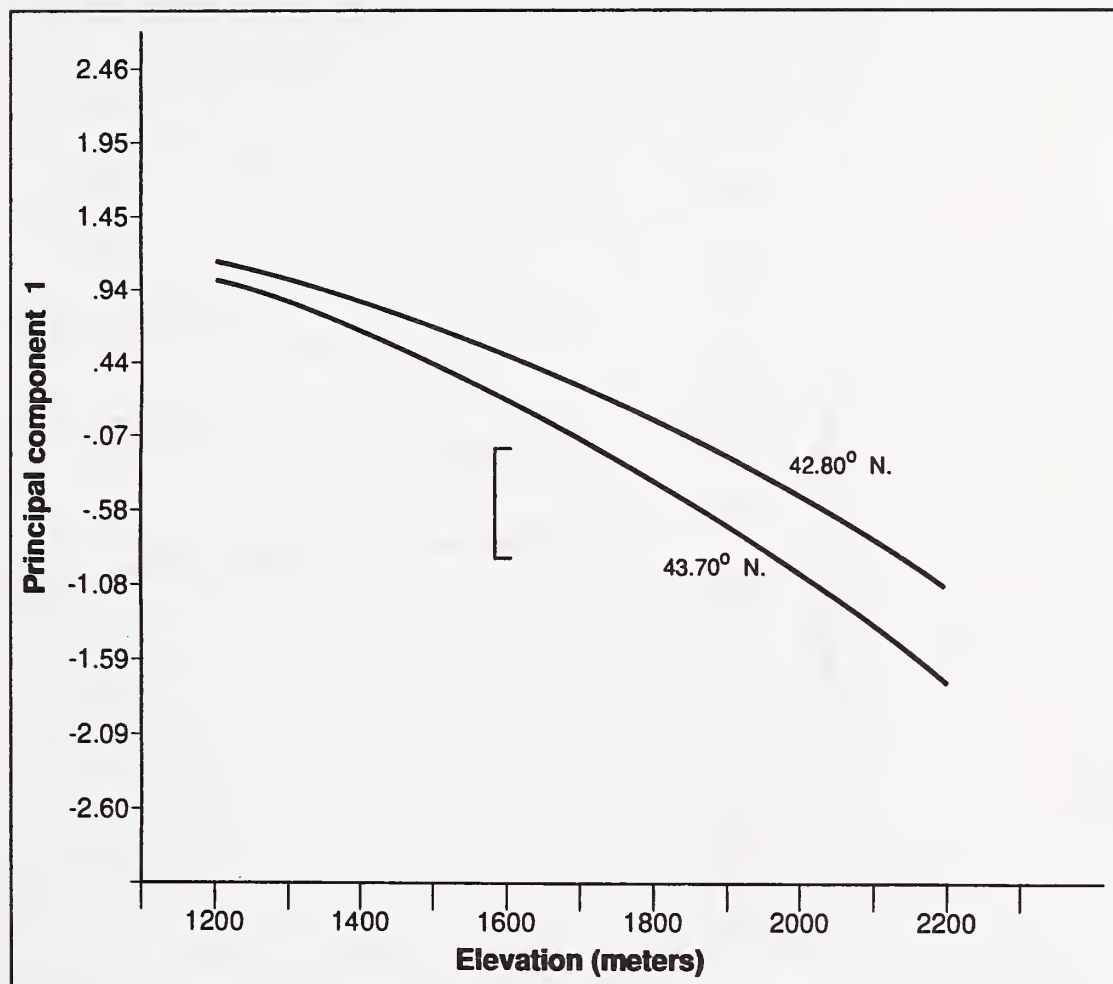


Figure 3—Relation between principal component 1 and elevation at two latitudes, other factors constant at slope = 7 percent and distance equal 75 kilometers east of Cascade crest. Vertical line is equal to one standard deviation of within-source additive genetic variance of principal component 1 and is equivalent to a transfer risk of 0.38.

From about 43.80° N., sample distribution was restricted to the east slopes of the Cascades (fig. 1), and gradients with distance from the crest were not apparent. South of 43.80° N., clines with distance were steepest or more curvilinear at low elevation (fig. 4), but in general the distance clines were weak.

Although the influence of slope was significant, its effect was small compared with standard deviation of within-source additive genetic variance.

Lack of fit to the regression model was very highly significant for PC-1 (table 7).

PC-2—The equation explained 36 percent of the source-related variation. The two largest standard coefficients were associated with the elevation \times latitude interactions (table 7). Between southern and central and central and northern Oregon, the slopes of the elevational clines reversed (fig. 5); these interactions persisted as far east as the samples extended.

The steepest latitudinal clines were at low and, to a lesser extent, high elevation (fig. 5). At intermediate elevations, where most lodgepole stands occur in the sample area, the latitudinal gradient was shallow. Gradients with distance also were weak when compared with the standard deviation of within-source additive genetic variation. Lack of fit was significant (table 7).

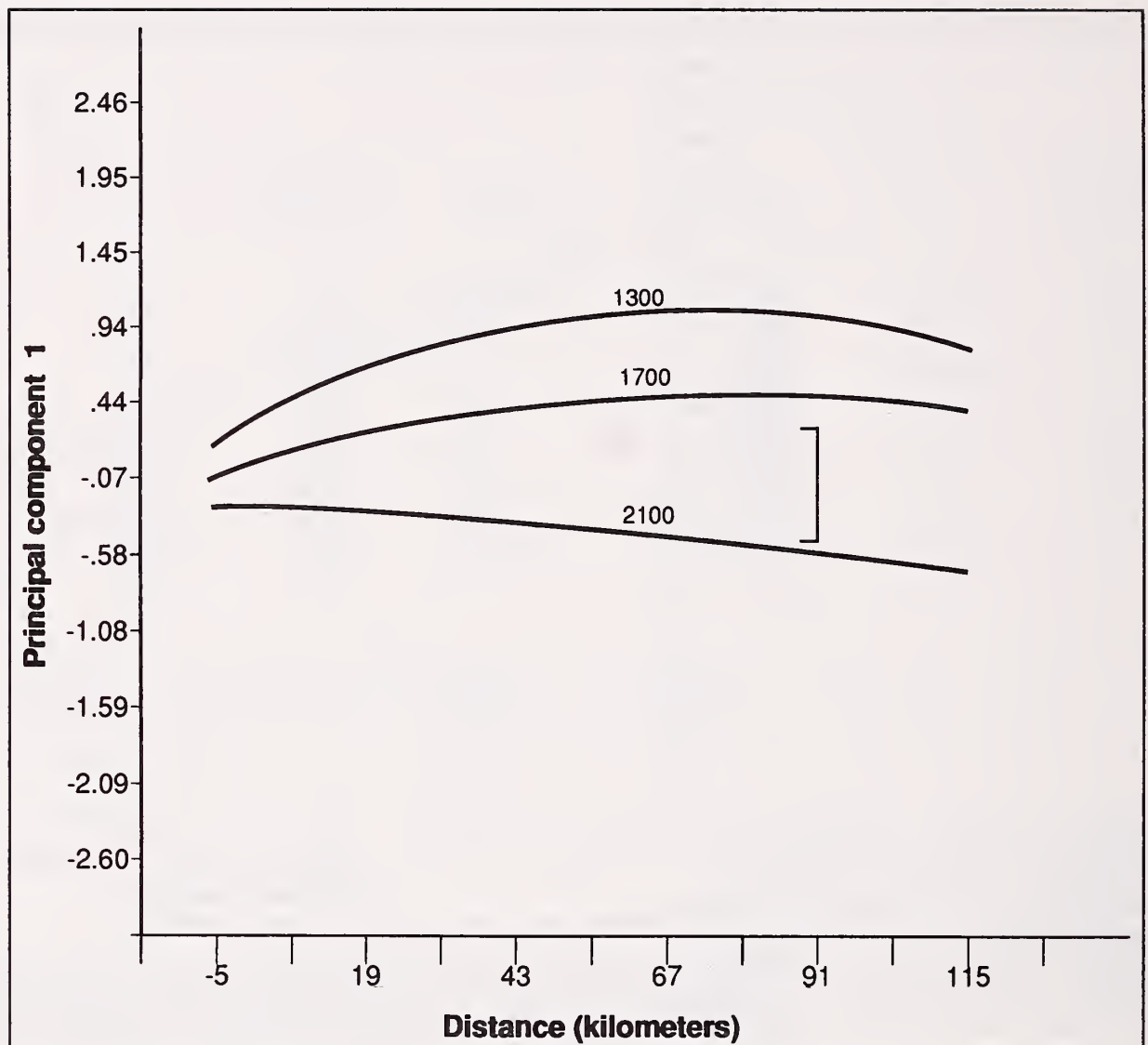


Figure 4—Relation between principal component 1 and distance from the Cascade crest at three elevations, other factors being constant at slope = 7 percent and latitude = 42.50° N. Vertical line is equal to one standard deviation of within-location additive genetic variance of principal component 1 and is equivalent to a transfer risk of 0.38.

Classification Analyses

These analyses were based initially on 24 seed zones (Tree Seed Zone Map 1973) subdivided into 300-m elevation bands for a total of 60 subzones. Current breeding units use elevation bands of 305 m.

Table 8 shows results of a classification analysis of factor scores for the principal components. Principal components separated the trait complex into a portion that had differentiated predominantly by elevation (FS-1 or size traits) and a portion that has differentiated also by latitude and distance from the Cascades (FS-2 or seed size and seedling form). For both principal components, $\sigma^2_{S/E/Z}$ was statistically significant ($F=2.38$, d.f.=129,83, $p<0.001$ for PC-1; $F=1.49$, d.f.=129,83, $p=0.026$ for PC-2), thereby indicating lack of fit to the classification model, as occurred with the regression model.

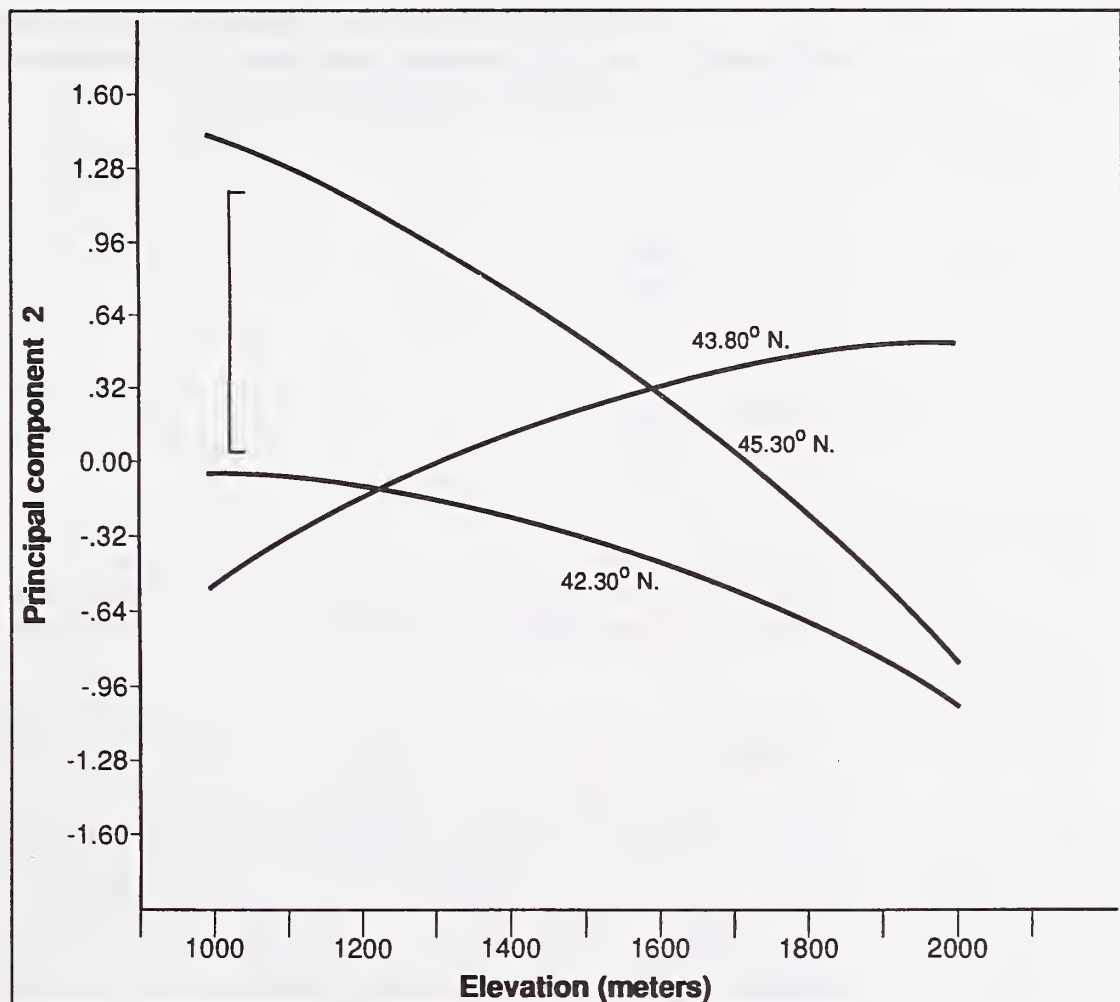


Figure 5—Relation between principal component 2 and elevation at three latitudes, other factors constant at slope = 7 percent and distance = 15 kilometers east of Cascade crest. Vertical line is equal to one standard deviation of within-location additive genetic variance of principal component 2 and is equivalent to a transfer risk of 0.38.

Results of the other classifications that were tried, including elevation bands of 200 and 400 m, flat vs inclined slopes, and various conifer groupings, are not included, because in no case did these classifications change the significance level for lack of fit.

Based on the regression analyses and mapping of variation using the regression equations, a grouping of the 24 original seed zones into seven larger zones or regions was chosen for further evaluation (fig. 1). Grouping resulted in a negative component of variance for the term "seed zones in regions." Otherwise, use of 7 regions instead of 24 zones did not change substantially the components of variance for the different levels of classification (table 8), including lack of fit. The only exception was that percentage of variance in FS-2 associated with regions increased compared with zones and the effect of elevation bands decreased.

Region 7 is based on few seed sources and is a valid unit only in the sense that it (Ochoco Mountains) is distinct from the east Cascades region (fig. 1). Also, only the eastern edges of zones 451, 452, 473, 493, 501, and 502 were sampled; regions these zones are assigned to included only the eastern edge of the zones.

Table 8—Percentages of source-related variance associated with seed zones, 300-meter elevation bands in zones, and sources within elevation bounds in zones

Trait	σ^2_Z	$\sigma^2_{E/Z}$	$\sigma^2_{S/E/Z}$
Current zones:			
Factor score-1	0 ^{ns a b}	67***	33***
Factor score-2	42**	23*	35*
Proposed zones:			
Factor score-1 ^c	0 ^{ns}	68***	32***
Factor score-2 ^c	55***	8 ^{ns}	37*

^a Values are in percent and equal 100 when summed horizontally.

^b Levels of significance are ns = $p > 0.05$; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

^c Shows percentages for factor scores after the 24 current seed zones have been combined in 7 proposed new zones or regions.

Classification based on both zones and regions and regression analyses were combined (Campbell 1991) in a final attempt to eliminate lack of fit to the models. In no case did this alter the significance of lack of fit. Stepwise entry of geographic terms from the regression model into the combined analysis indicated that only one term, EL (elevation \times latitude), was contributing to source variation within elevation bands in zones or in regions, and this was only for FS-1. The EL term had the largest standard coefficient in the regression equation relating FS-1 to geographic variables (table 7). The combined analysis simply showed that this interaction was still contributing to source-related variation within the subunits. The EL term had a partial $R^2 = 0.055$ when classification was based on the 24 zones, and 0.062 when based on the 7 regions. Zones apparently were grouped into regions in such a way that EL-variation within units was only marginally increased when unit size was increased.

Average seed transfer risk (R_w) was estimated for subzones and subregions (elevation bands in zones and elevation bands in regions). Values were 0.39 and 0.40, respectively. As noted earlier, I assumed that half of R_w represented sampling error of one type or another and half ($R_w = 0.20$) represented adaptive differences associated with random transfers among all locations with a subunit. The R was calculated from the regression equations for 10 random transfers between sample points in two of the elevation bands, 1450 to 1750 m and 1750 to 2050 m in region 5 (fig. 1). Fifteen sample locations were available within the lower band; 11 within the higher. Mean R -value for the 10 transfers within the lower band was 0.226 ± 0.115 (range, 0.112 to 0.451) and within the upper band 0.214 ± 0.145 (range, 0.037 to 0.520).

Discussion
Relations Among Traits

At the source level, emergence rate was negatively correlated with final height (mean $r = -0.512$ for the four environments) but the correlation was positive when based on families-in-sources (mean $r = 0.427$). Stephan (1980), who was studying a larger geographic range of var. *murrayana* sources, reports a negative correlation between seed weight and height growth. Other results also indicate that if the sample area spans mesic and xeric sites, seed weight and seedling size are negatively correlated; families from drier areas have heavier seeds but slower growing seedlings (Griffin and Ching 1977, Loopstra and Adams 1989, Sorensen 1983, Sorensen and others 1990). If the entire sample area is mesic, the correlation between seed size and seedling size may be positive at the source level (Campbell and others 1989). Presumably, large seeds and rapid germination both contribute to successful emergence and seedling establishment on summer-droughty sites.

A second trait pair that had contrasting correlations for sources and families-in-sources was elongation rate the second year and size at the end of the year. Elongation rate was in relative terms, $\text{cm} \cdot \text{cm}^{-1} \cdot \text{yr}^{-1}$. Plants with large values had elongated more than expected based on first-year height. For sources, the correlation was strong and positive (mean $r = 0.812$ for the four environments), but there was no correlation for families-in-sources (mean $r = -0.036$). This implies that a longer test would have increased source variance more than within-source variance.

Geographic Variation

The lodgepole sources in this test sampled an extensive elevational range. PC-1 and the size traits appear to be differentiated largely by elevation within seed zones (table 8). PC-2, which is composed of positive loadings from seed size and root weight and negative loading from relative elongation rate (table 4), also varied with elevation, but showed even closer association with latitude and distance (tables 6 and 8). From this I propose that the traits clustered under PC-1 are showing mainly an adaptive response to temperature, and under PC-2 they are showing a response to gradients in moisture availability or moisture stress. Field studies in older natural stands on xeric and mesic sites have shown that low soil moisture content in summer is associated with comparatively high allocation of primary production to the roots (Comeau and Kimmins 1989). For western Oregon Douglas-fir, production and turnover of fine roots was greater on dry than on moderate and wet sites (Santantonio and Hermann 1985). The common-garden results indicated that there is a genetic component to this pattern of assimilate allocation.

For PC-1 (the vigor or size PC), all the explained source-related variation in the classification analysis was associated with elevation (table 8, $\sigma^2_{S/E/Z}$ excluded). Elevation also was a factor in several of the terms having the highest standard coefficients in the multiple regression for PC-1 (table 7). Source elevation was cited in the northern Rocky Mountains as the dominant factor in lodgepole differentiation (Rehfeldt 1987). The importance of this term must be partly because of the wide elevational range occupied by the species and represented in the tests; for example, 750 m in central and southern British Columbia (Ying and others 1989), 1100 m in northern Idaho (Rehfeldt 1983), 1350 m in the Upper Snake River Basin of eastern Idaho and western Wyoming (Rehfeldt 1986), 1600 m in central Idaho (Rehfeldt 1985), and 1630 m in my test, including 1120 m within a single seed zone. According to Hopkins' bioclimatic "law" (Hopkins 1918), 122 m in elevation is equivalent to 1 degree of latitude, thereby making the elevation range of my samples comparable to a latitudinal distribution of about 13 degrees, or about the distance from Portland, Oregon, to the California-Mexican border.

Rehfeldt (1991) also emphasizes the relation between elevation and length of growing season. For central Oregon, Baker (1944) shows a linear relation whereby a 100-m change in elevation is equivalent to an 8.5-day change in growing season. The relation is based on few weather stations and none from the east side of the Cascades, and it does not account for the large differences in growing season length among stations of nearly the same elevation (table 2). It does indicate, nevertheless, that there should be a strong general relation between vigor or plant size and source elevation.

The relation between source elevation and seedling performance was not linear (table 7, figs. 3-5). Three hundred meters was selected as a general limitation for seed transfer, after evaluation of the term for lack of fit ($\sigma^2_{S/E/Z}$) using different band widths for elevation in the classification analyses. Rehfeldt also has reported non-linear relations between seed origin and seedling performance and, depending on the source location, recommends maximum elevational transfers of 100 to 350 m (Rehfeldt 1983, 1985, 1986). Ying and others (1989) suggest a maximum transfer of 350 m for interior British Columbia. Even for one species, the genetic change associated with elevation is dependent on the local situation, which makes generalization difficult.

Local Variation

Local variation may be due to chance or to selective factors. In the following, I discuss selective factors that might have a role in local differentiation of lodgepole in this area. For both principal components, variation among sources within elevation bands within seed zones ($\sigma^2_{S/E/Z}$) was significant in the classification analysis and amounted to about one-third of the total source-related variance (table 8). Adding other classes to the analysis had only a slight effect on this value. Likewise, in the regression analyses, lack of fit was significant (table 7), thereby indicating that distance, elevation, latitude, aspect, and slope variables did not fully characterize the adaptive genetic requirements of the sites. Adding topographic variables to the classification analysis reduced the sums of squares relatively little and did not reduce the size of the F-value for lack of fit. Except for EL, which accounted for about one-eighth of $\sigma^2_{S/E/Z}$ in the combined analysis of PC-1, no topographic variable had a partial $R^2 > 0.018$. Grouping seed zones into substantially larger regions (fig. 1) had minimal effect on $\sigma^2_{S/E/Z}$ (table 8). This suggested that lack of fit was not due to broad interactions within the subunits but was occurring at a local level.

Local topography in the sampled area was generally rolling (mean slope for sample sites was 7 percent). There were few streams and rivers or deep canyons. The most striking topographic features were "flats" of various size with associated cold air drainage or high water tables. Lodgepole pine in this area is cold hardy (Berntsen 1967, Cochran and Berntsen 1973, Sakai and Weiser 1973, Sorensen and Miles 1974, Stoneman 1984) and invariably was found on these sites, but such areas were not, contrary to my expectation, associated with seedling traits genetically differentiated from those in surrounding areas. Apparently, variation in cold hardiness (either as tolerance or avoidance) is not the main factor determining lack of fit to the models.

Given the observations that most lateral root development of young lodgepole pine is near the soil surface (Bishop 1962, Horton 1958) and reports that lodgepole is sensitive to moisture stress (Bates 1923, Gail and Long 1935 [original not seen, reported in Tarrant 1953], Leighty 1947, Stuart and others 1989), I propose that some lack of fit may be due to local topographic factors affecting moisture availability, but those topographic factors were not related to the geographic factors I measured. Weather records from stations in central Oregon show large and long deficits in summer and autumn moisture (table 2). For gently rolling, dry-land farming areas, it has been reported that topographic factors such as slope position and even slope form (concave vs convex curvature) and "associated pedological and microclimatological factors" can influence the length of time over which adequate moisture is available (Sinai and others 1981, Spratt and McIver 1972). I have no forestry references to indicate a similar situation exists in central Oregon; however, many of the lodgepole sites were xeric and gently rolling. If lodgepole is sensitive to moisture stress, these same or similar topographic factors causing local differences in upper soil moisture availability might account for part of the lack of fit.

Drought resistance has been compared for a wide-ranging group of provenances including one of var. *murrayana* (Dykstra 1974). In a glasshouse test, Dykstra found that provenances differ in the ability to grow and survive at increasingly negative water potentials. Stoneman (1984) investigated variation in drought tolerance by using a widely distributed subsample of his families. He evaluated several cell water components and found that families account for a significant proportion of the variation in some components, but genetic differences are not as obvious as in growth and frost hardiness. His sample distribution was not comparable to the level of topographic differences mentioned by Spratt and McIver (1972) and Sinai and others (1981), and he did not indicate which families (sources) contribute to the differences in cell water components.

This section will consider previous work in central Oregon, recommendations for breeding zone boundaries and for seed transfer in the absence of breeding programs, use of the regression model in seed transfer, and lack of fit to the models. The suggested guidelines are for the sample area depicted in figure 1 and are deemed provisional, because they are based on the genetics of seedling variation. Some aspects of the test indicated that source differentiation was still increasing when this study was terminated. Long-term plantation observations may later indicate needed modifications to zone boundaries.

One other seedling test evaluated adaptive variation in part of the sample area (Stoneman 1984). Stoneman's sampling was concentrated in seed zones 711 and the upper one-third of 702 with lighter sampling for another 15 to 30 kilometers north, west, and south. He measured growth and growth rhythm over 2 years, but also evaluated susceptibility to early autumn freeze damage. Growth potential and early autumn freezing injury were negatively correlated. Elevation of seed source had the greatest influence on genetic differentiation. Geographic effects independent of elevation were significant, but explained less of the variation in regression models than did elevation. Based on analysis of several individual traits, Stoneman's models suggested that "seed transfer can be relatively broad geographically" (1984). His most conservative estimate for width of the elevational band was 235 m.

Provisional Seed Transfer Guidelines

Previous Work

Breeding Zone Boundaries

My test also indicated that relatively broad geographic zones seem suitable for most of the east slopes of the Cascades and for the Warner Mountains. The regions imposed on figure 1 (numbers 1 through 6; Ochoco Mountains, number 7, excluded because of small sample size) range in size, based on lodgepole pine distribution only, from about 200 000 ha in the north and southeast to about 350 000 ha in the central part of the sample area. Region boundaries were based on previous seed zone delineation, but could be adjusted for the purpose of breeding zone designation. Plots using the regression equations could be examined to indicate where boundaries could be changed with least effect on seedling traits.

Elevation control is important. Seed transfer to a lower elevation will result in reduced growth potential; seed transfer to a higher elevation will lead to increased risk due to reduced hardiness (Stoneman 1984). Stoneman (1984) proposes an elevational interval of 235 m, but notes that the interval ranges from 235 to 450 m depending on trait (Stoneman 1984). My results indicated a band width of about 300 m, which probably should be maximum in the west-central and southwest parts of the sampled range. But it should be kept in mind that in some areas gradients become steeper as elevation increases (fig. 3). High-elevation sites presumably will not be part of breeding units, but if they are, the elevation bands should be narrower at high elevation.

Seed Movement and Transfer Risk

In general, the regression equations (table 7) should be the best guide in seed source selection (Rehfeldt 1990). In their use, factor scores are calculated for both the site to be regenerated and potential seed sources from inventory. Differences in values between planting site and seed sources are determined, and seed transfer risks are calculated from these differences relative to the standard deviations of the additive genetic variance of the factor scores.

An example of application is given in table 9 with one planting site and five potential seed sources. The example comes from the 1450- to 1750-m elevation band in region 5 (fig. 1). The planting site is low elevation (1460 m) near the west edge of block. Seed sources were chosen randomly from the other sample sites in the unit. The planting site also was a sample site. Seed source selection was based on the combined value for transfer risk (table 9, part B, far right column) as calculated from the regression equation (appendix). The best source has a calculated 5 percent in nonadapted or mismatched seedlings. It also has the highest factor score for plant vigor (FS-1 value in table 9), so seems the reasonable choice for the planting site.

The program for calculating transfer-risk estimates in table 9 is given in the appendix and also is available on diskette from the author (see inside front cover for address).

If seed stands are not kept separate in inventory, an alternative is to bulk well-distributed seed collections from a 300-m elevation band within a zone or region (fig. 1). Such bulked collections, and there could be several, can be used throughout that unit. If seed collections are indeed well distributed throughout the unit, then the transfer risk associated with the use of a bulked lot would be about equal to that calculated for the average within-unit transfer distance. The R_w value was estimated above to be about 20 percent.

Table 9—Calculating seed-transfer risks and seed source selection based on regression models^a

Location	Distance	Elevation	Latitude	Slope	
	<i>Kilometers</i>	<i>Meters</i>	<i>°N</i>	<i>Percent</i>	
A. Topographic variables for planting site and five potential seed sources.					
Planting site	39	1460	42.55	5	
Seed source:					
1	44	1460	43.01	0	
2	50	1690	42.49	5	
3	28	1560	43.19	2	
4	59	1510	42.65	5	
5	94	1580	42.62	5	
B. Values for factor scores 1 and 2 and for seed-transfer risks based on the 2 principal components computed individually and combined.					
	Scores		Transfer risk		
	FS-1	FS-2	FS-1	FS-2	Combined
Planting site	0.8027	−0.3731			
Seed source:					
1	.6578	−.2592	.0842	.0396	.1204
2	.5678	−.5845	.1358	.0724	.1984
3	.2082	−.0044	.3362	.1256	.4196
4	.8301	−.4597	.0170	.0304	.0468
5	.7516	−.6022	.0304	.0784	.1064

^a Seed-transfer risks are the estimated proportion of nonadapted seedlings in the seed source populations relative to the local population when used at the designated planting site.

Lack of Fit

Lack of fit was described earlier as source variance that was not described by the models. In this sample area, lack of fit to both regression and classification models was significant for both principal components, thereby suggesting that seed transfer could involve risk of maladaptation even if the models were followed. Calculation of risk associated with the mean transfer distance within units and evaluation of a number of transfers between sample sites indicated, however, that risks were acceptable, based on the assumptions of the model.

Conclusion

It seems that use of seeds bulked by 300-m bands within the regions shown in figure 1 involved acceptable risk of nonadaptation. The risk can be reduced somewhat if seed lots are inventoried separately, but that may not be worth the effort unless specific stands already are set aside for seed production. Then, it might be advisable to collect from large numbers of trees within each stand and use the program based on the regression equations (appendix) to determine the best match between seed stand and planting site.

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Conversion Table

When you know:	Multiply by:	To find:
Centimeters (cm)	0.394	Inches
Meters (m)	3.281	Feet
Hectares (ha)	2.471	Acres
Celcius (°C)	1.8 and add 32	Fahrenheit

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Appendix

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10 REM THIS PROGRAM COMPUTES A "RISK" VALUE ASSOCIATED WITH SEED-TRANSFER
20 REM OF LODGEPOLE PINE. THE VALUE RANGES FROM ZERO
30 REM TO ONE. ZERO INDICATES A SEED SOURCE IN WHICH ALL SEEDLINGS ARE WELL
40 REM ADAPTED TO THE PLANTING SITE; ONE INDICATES A SOURCE IN WHICH ALL
50 REM SEEDLINGS ARE HYPOTHETICALLY POORLY ADAPTED TO THE PLANTING SITE.
60 REM VALUES FOR THE FOLLOWING ENVIRONMENTAL-INDEX VARIABLES ARE REQUIRED
70 REM FOR BOTH THE SEED ORIGIN AND THE PLANTING SITE:
80 REM E = ELEVATION IN METERS(LIMITS=LOCAL PLUS OR MINUS 450)
90 REM L = LATITUDE IN DEGREES(LIMITS=36.00 TO 48.00)
100 REM D = DISTANCE WEST FROM CASCADE CREST IN KM (EAST IS NEGATIVE)(LIMITS=
110 REM 75 TO -15)
120 REM
130 REM I. OBTAIN ENVIRONMENTAL-INDEX VALUES FOR THE SEED SOURCE
140 INPUT " THE ELEVATION OF THE SEED SOURCE IS ",ELEV
150 INPUT " THE LATITUDE OF THE SEED SOURCE IS ",LAT
160 INPUT " THE DISTANCE FROM CASCADE CREST OF SEED SOURCE IS ",DIS
162 INPUT " THE SLOPE IN PERCENT IS ",SLO
170 REM II. CALCULATE FACTOR SCORE FOR FIRST PRINCIPAL COMPONENT(FS1 AND F1)
180 LET M=0
190 LET L=LAT-40
210 LET E=(ELEV-800)/10
214 LET D=DIS
216 LET S=SLO/100
220 LET B1=3.68E-02*E
230 LET B2=-2.02E-02*S
240 LET B3=-2.4E-04*D*D
250 LET B4=1.63E-02*D*L
260 LET B5=-2.45E-02*E*L
270 LET B6=-1.65E-06*D*E*E
272 LET B7=1.69E-06*D*D*E
274 LET B8=-2.24E-03*D*L*L
276 LET B9=2.81E-03*E*L*L
278 LET B10=2.12E-04*L*S*S
280 LET B0=7.15E-01
290 LET F1=B0+B1+B2+B3+B4+B5+B6+B7+B8+B9+B10
300 REM II. CALCULATE FACTOR SCORE FOR SECOND PRINCIPAL COMPONENT(FS2 AND F2)
310 LET C1=-9.46E-03*D
320 LET C2=-1.32E-01*E
330 LET C3=-5.37*L
340 LET C4=-1.06E-04*E*E
350 LET C5=7.84E-01*L*L
360 LET C6=8.69E-02*E*L
370 LET C7=4.96E-07*D*D*E
380 LET C8=-1.2E-02*E*L*L
390 LET C0=8.24
400 LET F2=C1+C2+C3+C4+C5+C6+C7+C8+C0
410 IF M>0 THEN 530
420 LET M=M+1
430 LET FS1=F1
440 LET FS2=F2
450 PRINT E;L;D;S;FS1;FS2
460 PRINT
470 REM IV. OBTAIN ENVIRONMENTAL-INDEX VALUES FOR THE PLANTING SITE
480 INPUT "THE ELEVATION OF THE PLANTATION IS ",ELEV
490 INPUT "THE LATITUDE OF THE PLANTATION IS ",LAT
500 INPUT " THE DISTANCE FROM CASCADE CREST OF THE PLANTATION IS ",DIS
505 INPUT "THE SLOPE IN PERCENT IS ",SLO
510 REM V. CALCULATE X1= DIFFERENCE BETWEEN SOURCE AND PLANTATION IN FIRST PC
520 GOTO 190
530 LET X0=FS1-F1
540 LET X1=X0/2
```

```

550 REM VI. CALCULATE NORMAL DEVIATE CORRESPONDING TO X1 (Z1)
560 REM SA1= STANDARD DEVIATION FOR ADDITIVE GENETIC VARIANCE FOR FACTOR
570 REM SCORE 1
580 LET SA1=.6837
590 LET Z1=X1/SA1
600 IF Z1<0 THEN 630
610 LET SIGN=1
620 GOTO 640
630 LET SIGN=-1
640 LET Z3=Z1*SIGN
650 LET N=0
660 REM VII. CALCULATE AREA UNDER STANDARD NORMAL CURVE FROM 0 TO Z
670 LET A1=.387416*Z3
680 LET A2=.0458442*Z3*Z3
690 LET A3=-.140874*Z3*Z3*Z3
700 LET A4=.0574989*Z3*Z3*Z3*Z3
710 LET A5=-9.845671E-03*Z3*Z3*Z3*Z3*Z3
720 LET A6=6.33339E-04*Z3*Z3*Z3*Z3*Z3*Z3
730 LET A0=6.90589E-04
740 LET A=A0+A1+A2+A3+A4+A5+A6
750 IF N>0 THEN 970
760 LET N=N+1
770 LET R1=A*2
780 IF R1<=0 THEN 810
790 GOTO 820
800 GOTO 820
810 RF1=0
820 RF1=R1
830 REM VIII. CALCULATE X2= DIFFERENCE BETWEEN SOURCE AND PLANTATION IN 2ND PC
840 LET X2=FS2-F2
850 LET X3=X2/2
860 REM IX. CALCULATE NORMAL DEVIATE CORRESPONDING TO X2 (Z2)
870 REM SA2 = STANDARD DEVIATION OF ADDITIVE GENETIC VARIANCE FOR FACTOR
880 REM SCORE 2
890 LET SA2=1.1618
900 LET Z2=X3/SA2
910 IF Z2<0 THEN 940
920 LET SIGN1=1
930 GOTO 950
940 LET SIGN1=-1
950 LET Z3=Z2*SIGN1
960 GOTO 670
970 LET R2=A*2
980 GOTO 1010
990 GOTO 1010
1000 R2=0
1010 RF2=R2
1020 REM X. CALCULATE THE "RISK"(CRF) .
1030 LET CRF=RF1+RF2-(RF1*RF2)
1040 PRINT E;L;D;S;F1;F2
1050 PRINT
1060 PRINT RF1;RF2;CRF
1070 PRINT "THE RISK VALUE IS ";CRF
1080 END

```


Sorensen, Frank C. 1992. Genetic variation and seed transfer guidelines for lodgepole pine in central Oregon. Res. Pap. PNW-RP-453. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 30 p.

Cones were collected from 272 trees at 189 locations uniformly distributed over the east slopes of the Oregon Cascade Range and Warner Mountains. Variation in seed and seedling traits was related to (1) seed source latitude, distance from the Cascade crest, elevation, slope, and aspect in multiple regression analyses; and (2) seed zone and elevation band in classification analyses. Provisional seed transfer guidelines are presented. These include a regression equation for guiding seed transfer and estimating transfer risk, and a new outline of fixed seed zones.

Keywords: *Pinus contorta* var. *murrayana*, lodgepole pine, geographic variation, seed transfer, breeding zones.

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